

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Mammalogy Papers: University of Nebraska State
Museum

Museum, University of Nebraska State

1970

Chiropteran Systematics

J. Knox Jones Jr.

University of Kansas Main Campus

Hugh H. Genoways

University of Nebraska - Lincoln, h.h.genoways@gmail.com

Follow this and additional works at: <http://digitalcommons.unl.edu/museummammalogy>



Part of the [Biodiversity Commons](#), [Terrestrial and Aquatic Ecology Commons](#), and the [Zoology Commons](#)

Jones, J. Knox Jr. and Genoways, Hugh H., "Chiropteran Systematics" (1970). *Mammalogy Papers: University of Nebraska State Museum*. 187.

<http://digitalcommons.unl.edu/museummammalogy/187>

This Article is brought to you for free and open access by the Museum, University of Nebraska State at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Mammalogy Papers: University of Nebraska State Museum by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Reprinted from ABOUT BATS, Slaughter and Walton, Eds.
Published by Southern Methodist University Press, 1970. Dallas, Texas 75222

Chiropteran Systematics

J. KNOX JONES, JR. and HUGH H. GENOWAYS

With few exceptions, the systematic arrangement of bats above the level of species and genera was erected on the basis of classical studies of structure of the bony skeleton (principally the wing, shoulder girdle, sternum, and cranium), and to a lesser extent on development and structure of the teeth (see especially Dobson, 1878, and Miller, 1907). At the generic and specific levels of classification, external and cranial features have been stressed as well as dental structure and dental formulae. In recent years, with the development of the so-called bio-systematic approach to studies of relationships among animals and plants, new techniques such as serological investigations, analyses of karyotypes, comparison of ecto- and endoparasitic faunas, and investigations of a variety of specialized morphological structures of both the soft and hard anatomy have added considerably to our understanding of chiropteran systematics and phylogeny, but much yet remains to be learned.

The number of published studies relating to systematics of bats has annually increased at a rapid rate over the past several decades. This has resulted from greater opportunities for field and laboratory studies than in the past and a concomitant increase in number of investigators, and also because of new and better methods of acquiring specimens (mist nets and sophisticated bat traps, for example). It may be expected that the study of chiropteran systematics will reach an even greater level of growth in the decades immediately ahead.

In the sections that follow, our aim has been to allude to problems at several levels of bat classification, by way of example, and to mention ways in which some of the newer techniques have aided in the solution of certain systematic problems. Each of the other papers in this symposium will raise additional cogent points relevant to a better understanding of the classification and systematics of bats.

FOSSIL BATS

Excepting for Pleistocene and sub-Recent remains, fossil bats are poorly known, a fact reflected by the questionable assignment of certain extant groups at the higher levels of classification. The earliest known fossil bat is *Icaronycteris index* from the early Eocene of Wyoming (Jepsen, 1966). This amazingly well preserved specimen is, morphologically speaking, a perfectly good bat and yields no real clues as to the mode of origin of flight. It was placed in a new family, *Icaronyc-*

teridae, in the suborder Microchiroptera although in at least one characteristic, presence of a claw on the index finger, it resembles members of the Megachiroptera. However, Jepsen noted that the specimen clearly resembles, and therefore presumably is more closely allied phylogenetically to, the living Microchiroptera based on structure of the teeth and shoulder articulation and many other anatomical features. Two other families that contain only fossil members from the middle Eocene of Europe are Archaeonycteridae and Palaeochiropterygidae. The relationships of these three fossil families to Recent families of microchiropterans still is unclear, as are the relationships of several early fossil genera, known from fragmentary remains, that cannot be assigned certainly to any family, fossil or Recent (see Koopman & Jones, this volume).

The first genera of fossil bats assignable to Recent families are from the late Eocene and early Oligocene of Europe; these include representatives of the families Emballonuridae, Megadermatidae, Rhinolophidae, and Vespertilionidae. The earliest record of the family Pteropodidae is from the middle Oligocene of Europe and that of the family Molossidae is from the late Oligocene of Europe. The earliest record of a Recent family of bats from North America is of a vespertilionid from the middle Oligocene and the earliest unquestioned occurrence of a phyllostomatid is in late Miocene deposits of northern South America. Several Recent families (Natalidae, for example) are represented in the fossil record only in Pleistocene deposits and seven families are presently known only by Recent representatives.

Because the earliest known chiropteran fossils are well-developed bats, there are no "intermediate" forms that provide evidence as to the ancestry and mode of evolution for flight of this unique mammalian order. Dental characteristics seem clearly to relate bats to insectivores, from which group they may have evolved in earliest Tertiary times. Probably bats were derived from some line of arboreal insectivores, passing through a gliding stage on the way from scansorial locomotion to true flight. The early bats may well have been crepuscular, or even diurnal, adapting at least partially in response to an untapped source of food. Megachiropterans still are basically crepuscular and all but a few lack the means to echolocate, suggesting that the nocturnal habits and echolocatory powers of the Microchiroptera could have developed after true flight was achieved.

SUBORDERS AND SUPERFAMILIES

Dobson (1875) was the author of the two subordinal names of bats—Megachiroptera for the Old World frugivorous and nectar-feeding bats of the family Pteropodidae, and Microchiroptera for the remaining

members of the order. Because these two groups of mammals are volant, they have been assumed by most workers to fall naturally into the same order, in that they are presumed to have arisen from a common ancestral stock. Still, when the two groups are compared, the most striking similarities are in the manner of locomotion and adaptations related thereto. Even then, the two differ in a number of structural features, but these perhaps logically can be attributed to divergence at an early stage in bat evolution with subsequent differential development. The index finger of most megachiropterans retains a claw and a degree of independence from the third digit uncharacteristic of microbats; for example, the humerus is relatively unspecialized, and the "whole general appearance of the skull is more nearly that of an ordinary mammal and less distinctively that of a bat" (Miller, 1907:44). The question arises, then, as to whether the order Chiroptera might possibly be diphyletic, with the two great groups representing convergent evolution attendant with development of aerial locomotion. Certainly this hypothesis is deserving of consideration, although it may be impossible to resolve the matter satisfactorily without an adequate fossil record.

Megachiropterans differ from microchiropterans in at least two important features unrelated to the skeleton. One of these, as reported by Mossman (1937, 1953), is that the fetal membranes are fundamentally different. A small, free yolk sac that becomes solid and gland-like is present in megachiropterans, whereas in the Microchiroptera a large yolk sac is present that undergoes incomplete inversion similar to that of primitive rodents. Also, the disc in Megachiroptera is mesometrial (as opposed to antimetrial), and the placenta is of the hemochorial type. In connection with the last point, some Microchiroptera also have hemochorial placentas, but others have the endothelio-chorial type, and still others are transitional between the two. Mossman (1953:296) noted the same kind of "wide divergence" in major subgroups of several other orders—Insectivora, Primates, and Edentata.

A striking difference is found in means of orientation between the two groups. Megachiropterans have small, simple ears that lack a tragus (a structure present in all Microchiroptera except rhinolophids), and have large protruding eyes. Orientation in most megabats is strictly visual in contrast to the highly developed echolocatory powers of microchiropterans, and most species presumably are crepuscular. However, a primitive type of echolocation has developed in *Rousettus* (perhaps the most primitive living genus of the suborder); these bats orient visually when light is available, but emit audible "clicks" in total darkness (Griffin, 1958; Vincent, 1963). Sounds made by *Rousettus* are

produced by the tongue, rather than by the larynx as in microchiropterans. Not all megachiropteran genera have yet been tested as to echolocatory powers, but of the significant number that have been studied only *Rousettus* is so endowed. It is of note that *Rousettus* is one of the few, if not the only, megachiropteran regularly to seek daytime retreats in total darkness. Whatever the significance of the differences in orientation, it is clear that most megachiropterans do not echolocate, and those few that do, have independently developed a distinctly different system from that found in the microbats.

At the superfamilial level in the Microchiroptera, the classification seems fairly stable at the moment with recognition of the four superfamilies: Emballonuroidea, Rhinolophoidea, Phyllostomatoidea, and Vespertilionoidea. One obvious problem, however, is the current placement of the fishing bats (Noctilionidae) with the Emballonuroidea. In many features the noctilionids resemble phyllostomatids and may well be placed ultimately in the Phyllostomatoidea.

FAMILIES AND SUBFAMILIES

At the familial level, a number of interesting problems remain to be solved. Some authors, for example, recognize the rhinolophids and hipposiderids as distinct families, while others merge these two as subfamilies of the single family Rhinolophidae.

The vampire bats of the nominal family Desmodontidae are of particular interest. That vampires are related to another New World group, the Phyllostomatidae, has long been recognized, but owing to unusual modifications associated primarily with sanguineous food habits, vampires have been regarded as representing a distinct family. In a recent paper in *Systematic Zoology*, Forman *et al.* (1968) reported that studies of the serology, chromosomes, and sperm morphology all indicate a close relationship between desmodontids and phyllostomatids.

Immunologic and electrophoretic tests revealed that *Desmodus* is more closely related to some members of the Phyllostomatidae than are certain phyllostomatids to each other. Of the species tested, *Desmodus* showed the highest affinities with the glossophagine genus *Choeronycteris* and with the phyllostomatines *Chrotopterus* and *Phyllostomus*. The data on karyotypes generally support, and in no way refute, the close relationships between vampire bats and phyllostomatids. Three subfamilies, Phyllostomatinae, Glossophaginae, and Stenoderminae, have members with diploid and fundamental numbers of chromosomes similar to those of *Desmodus* and *Diaemus*. As concerns sperm morphology, *Desmodus* and *Diphylla* were shown to be notably similar in general structure to representatives of five subfamilies of phyllostomatids (see

Fig. 3). These authors concluded: "Evidence from immunologic and karyotypic comparisons and studies of morphology of spermatozoa, suggests that vampire bats should be classified as a subfamily within the Phyllostomatidae."

Additional evidence based on host-ectoparasite relationships (Machado-Allison, 1967) closely ally the desmodontids with the phyllostomatids, as do the structure of the pectoral and pelvic girdles (Walton & Walton, 1968), and the similarity in acoustic orientation (Novick, 1963).

If the vampire bats are relegated to subfamilial status within the Phyllostomatidae, however, such an arrangement necessitates re-examination of the status of the current subfamilies of that group, numbering seven—more than in any other family of bats and stressing the unique diversity within this taxonomic unit. For one thing, the nominal subfamily Sturnirinae (represented by the single genus *Sturnira*) should be merged with the Stenoderminae, to which it possibly is linked by the Antillean genus *Brachyphylla*. (Silva-Taboada & Pine, 1969, however, regarded *Brachyphylla* as a member of the subfamily Phyllonycterinae on the basis of certain morphological and behavioral characters.) For another, the subfamily Chilonycterinae (including the three nominal genera *Mormoops*, *Chilonycteris*, and *Pteronotus*) probably deserves familial rank owing to a number of morphological and behavioral differences from other members of the Phyllostomatidae (see, for example, Dalquest & Werner, 1954, on the histology of the facial area of bats). The whole problem of chilonycterine relationships currently is under study by James D. Smith.

A unique problem is found in the subfamily Glossophaginae in that recent research indicates this nectar-feeding group could be polyphyletic. At any rate, the subfamily seems clearly to be composed of two groupings of genera, one characterized by *Glossophaga* and the other by *Choeronycteris*. Recent karyotypic studies by Baker (1967) indicate such a break, as do unpublished data by J. D. Gerber on serological relationships. Baker's data, however, seem to relate the *Glossophaga* section to phyllostomatines and the *Choeronycteris* section to the Carolliinae, whereas Gerber's findings, based on immunodiffusion and disc electrophoresis techniques, indicated the reverse. Current studies by Carleton J. Phillips on milk and permanent dentition of glossophagines and the basi-cranial structure of the skull also indicate two groupings of genera. Clearly there is a need for additional study of this intriguing problem.

Some of the other fields of study that have been used in recent years to elucidate relationships among bats at the familial level are functional

morphology (Vaughan, 1959), echolocatory ability (Novick, 1962, 1963, and others), comparative endocrinology and physiology (see, for example, Valdivieso *et al.*, 1968), and brain size (Findley, 1969). Although the latter two studies were preliminary in nature, they suggest stimulating areas for future investigations.

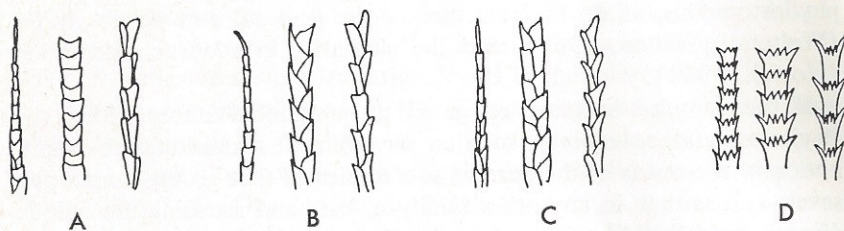


FIG. 1. Cuticular structure of distal (left), middle (center), and basal (right) parts of middorsal hairs of four species of bats: A, *Myotis leibii*; B, *Myotis velifer*; C, *Plecotus townsendii*; D, *Tadarida macrotis*. (After Miles, 1965).

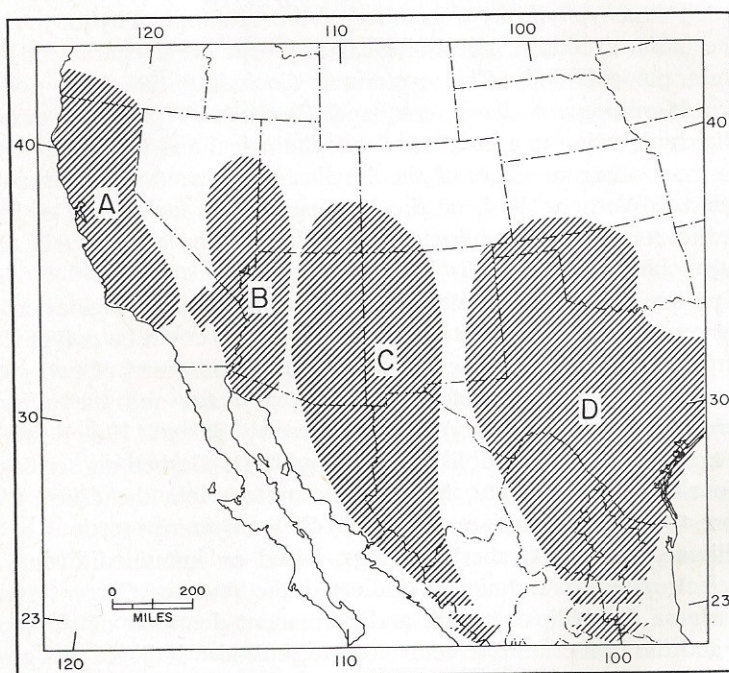


FIG. 2. Map indicating approximate limits of behaviorally (and probably genetically) segregated breeding populations of *Tadarida brasiliensis* in the southwestern United States. A breeding population on Baja California is not indicated. (Modified after Cockrum, 1969).

GENERA

Systematics at the generic level in bats traditionally has been based primarily on cranial, external, and especially dental characteristics. In at least some groups, earlier workers appear to have stressed relatively minor differences (in dental structure and formulae for example), at the expense of overwhelming evidence of similarity, resulting in an overabundance of generic names. Even with the advent of Miller's (1907) classic study of the families and genera of bats, many groups remained split at the generic level to a much greater degree than necessary. The trend in recent years has been, upon detailed study of related groups, to reduce the number of recognized bat genera.

Handley (1959), for example, synonymized the New World big-eared bats of the genera *Corynorhinus* and *Idionycteris* with the Old World genus *Plecotus*, but retained all three as distinct subgenera. The same author (1960) submerged the yellow bats of the nominal genus *Dasypterus* with *Lasiurus*, and commented (1960:473): "It seems more reasonable to stress the important similarities of these bats and regard them as congeneric, rather than to stress the insignificant differences and regard them as representing distinct genera. I do not believe that *Dasypterus* is useful even as a subgenus." The two had been separated principally on the basis of absence in *Dasypterus* of the minute first upper premolar present in most individuals of *Lasiurus*. Similarly, Cabrera (1958) placed the nominal molossid genus *Cynomops* as a subgenus of *Molossops* (*Cynomops* has two pairs of lower incisors as compared to one in *Molossops* and the third molars are simplified) and regarded *Mormopterus* as a subgenus of *Tadarida*. Most species of *Mormopterus* lack the minute first upper premolar (P2) present in *Tadarida* and have smaller ears.

An especially interesting case is provided by the monotypic vespertilionid genus *Pizonyx*, endemic to a restricted area in western North America and adapted for catching fish and small crustaceans. *Pizonyx* differs from *Myotis* principally in having large feet with long, flattened claws and in the possession of a large glandular mass in the wing membrane near the middle of the forearm; also, according to G. Lawrence Forman (personal communication), although the stomachs of *Pizonyx* and *Myotis* are grossly similar, that of *Pizonyx* is relatively larger and is markedly different in the extent of various zones of the gastric mucosa. The two are similar in other ways, including teeth and bacula, and Baker & Patton (1967) found the karyotype of *Pizonyx* to be identical with those of species of *Myotis* studied by them. These authors concluded that *Pizonyx* should be regarded only as a subgenus of *Myotis*.

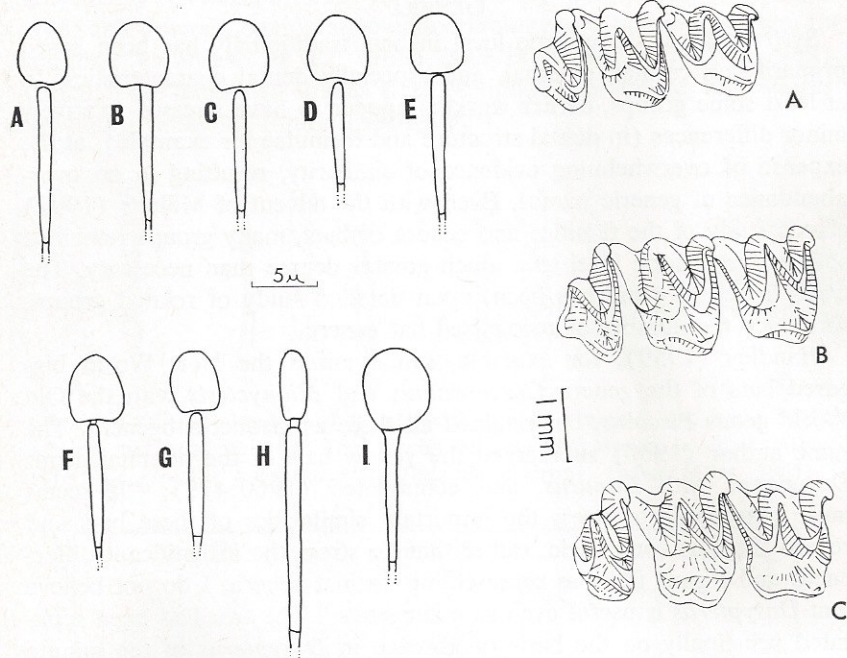


FIG. 3. Heads and midpieces of spermatzoa of some New World Chiroptera: A, *Desmodus rotundus* (Desmodontinae); B, *Diphylla ecaudata* (Desmodontinae); C-G, representative phyllostomatids; H, *Myotis volans* (Vespertilionidae); I, *Molossus molossus* (Molossidae). Note the similarity of structure between the two desmodontines and other phyllostomatids. (After Forman *et al.*, 1968).

FIG. 4. Right upper molar rows of four related species of *Myotis*, indicating differences in size and shape of teeth: A, *Myotis milleri*; B, *Myotis evotis*; C, *Myotis auriculus*; D, *Myotis keenii*. (After Genoways & Jones, 1969).

Similarly, Gardner & O'Neill (1969) recently placed the nominal South American genus *Corvira* as a subgenus of the widespread Neotropical genus *Sturnira* on the basis of "close external, cranial, and chromosomal similarities." Handley (1966) reduced the long-tongued genus *Musonycteris* to synonymy under *Choeronycteris* because he found the disparity in rostral proportions between the two (which was the principal basis for recognition of *Musonycteris*) to be less than between species in the related genus *Choeroniscus*.

A particularly cogent case in point is that of the generic name

Anamygdon, proposed by Troughton (1929) as a representative of the vespertilionid subfamily Kerivoulinae on the basis of a single specimen from the Solomon Islands. Phillips & Birney (1968) recently have demonstrated not only that *Anamygdon* is a synonym of *Myotis*, but that *A. solomonis* is inseparable from the earlier-described *Myotis adversus moluccarum*. Troughton erred in his interpretation of Miller's (1907) description of the differences between sterna of kerivoulines and vespertilionines (see Fig. 5), and thus was led to propose the new generic name.

Despite the trend to recognition of fewer genera than in the past, new generic names for bats continue to appear. Peterson (1965a), for example, named the free-tailed genus *Neoplatymops* from South America, distinguishing it from *Molossops* on the basis of a number of external, cranial, and dental peculiarities, especially presence of wart-like granulations on the forearm, two (instead of one) upper premolars, and a noticeably flattened skull. Hill (1964) named the phyllostomatine *Barticonycteris* from British Guiana, but Koopman & Cockrum (1967) arranged this name under *Micronycteris*, presumably as a subgenus. More recently, McKean & Calaby (1968) described a new genus of vespertilionid, *Lamingtona*, from New Guinea.

Many problems remain at the generic level in chiropteran systematics such as relationship among vespertilionine groups—the cosmopolitan

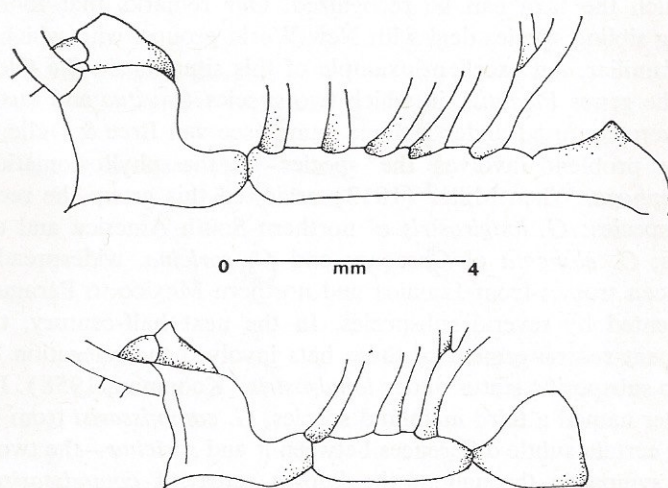


FIG. 5. Diagrammatic view of the ventro-lateral aspect of typical vespertilionine (upper) and kerivouline sterna. (After Phillips & Birney, 1968).

genus *Myotis* and the *Pipistrellus-Vespertilio-Eptesicus* complex, for example. Re-study of old material as well as development of new techniques and approaches will help to shed light on many of the existing problems.

SPECIES AND INFRASPECIFIC VARIATION

Characters by which species of bats, as other mammals, ordinarily are recognized include such features as external and cranial size and proportions, minor modifications of teeth and other hard parts, color, hair structure, and various differences in the soft anatomy. It should be stressed, however, that at the specific level these are only "taxonomic characters," that is, means by which the taxonomist can recognize and define the various species. Reproductive isolation (actual or potential), or the lack of it, is the ultimate test of specific distinction between members of different populations.

The number of recognized bat species has declined slightly over the past few years, the nominal kinds found not to be distinct at the specific level from other named taxa being partially offset by description of new species and resurrection from incorrect synonymy of others. Some of the most interesting problems in speciation involve so-called sibling species, two or more reproductively isolated units that resemble each other morphologically to a degree that they are difficult to distinguish, at least in early stages of taxonomic investigation. Detailed study of such complexes usually reveals a broad array of characters, many albeit cryptic, by which the taxa can be recognized. Our remarks that follow concerning sibling species deal with New World groups, with which we are most familiar. An excellent example of this situation in the Old World is in the genus *Plecotus*, in which two species (*auritus* and *austriacus*) long were confused under a single name (see van Bree & Dulic, 1963).

One problem involves the species of the phyllostomatid genus *Glossophaga*. When Miller (1913) reviewed this group, he recognized three species: *G. longirostris* of northern South America and adjacent islands; *G. elongata* of Curaçao; and *G. soricina*, widespread in the American tropics from Jamaica and northern Mexico to Paraguay, and represented by several subspecies. In the next half-century, the only significant rearrangement of these bats involved the relegation of *elongata* to subspecific status under *longirostris* (Koopman, 1958). In 1962, Gardner named a third mainland species, *G. commissarisi* from Mexico, noting certain subtle differences between it and *soricina*—the two species being sympatric throughout the known range of *commissarisi*. Upon critical study of specimens of the genus from the North American tropics, still another sibling, *G. alticola*, was discovered; *alticola*, origi-

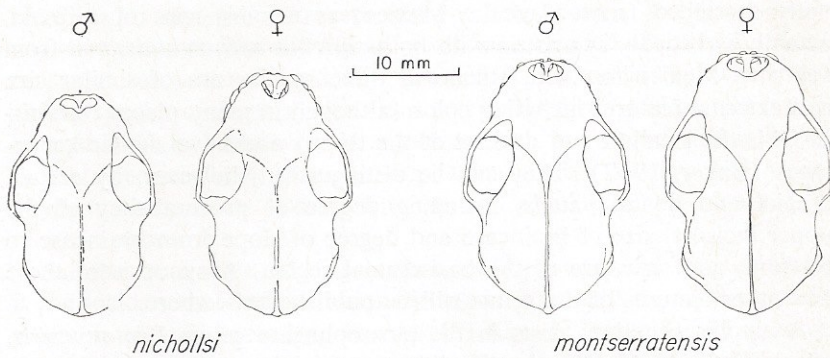


FIG. 6. Dorsal view of crania of adult *Ardops nichollsi* illustrating secondary sexual variation. Overall infraspecific variation in cranial size also is indicated in that the subspecies *A. n. nichollsi* is the smallest race of the species and *A. n. montserratensis* is the largest. (After Jones & Schwartz, 1967).

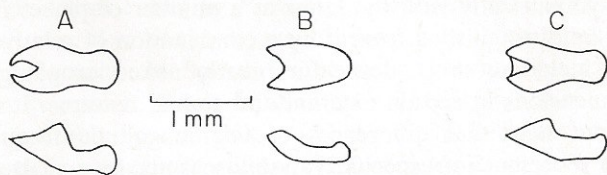


FIG. 7. Dorsal and lateral views of bacula of three related species of *Myotis*: A, *Myotis evotis*; B, *Myotis auriculus*; C, *Myotis keenii*. (After Genoways & Jones, 1969).

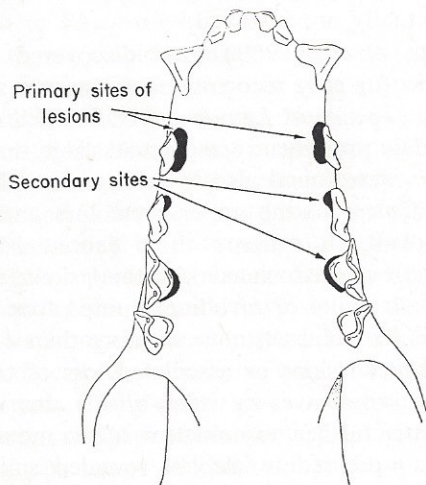


FIG. 8. Diagrammatic illustration of sites of lesions in the hard palate of *Leptonycteris nivalis*. The lesions are caused by a mite, *Radfordiella* sp., that evidently does not infest the related *Leptonycteris sanborni*.

nally described from Tlaxcala, Mexico, as a subspecies of *soricina*, actually is broadly sympatric with both *soricina* and *commissarisi* from southern Mexico to Costa Rica. All three species are of similar size and external features including color (although in many places *commissarisi* is the smallest and darkest of the three) and have similar karyotypes (Baker, 1967). They can be distinguished, however, by certain cranial and dental details, including degree of procumbancy of the upper incisors, size of braincase and degree of slope from braincase to rostrum, and structure of the basi-cranial region. A synopsis of these and other features of the genus will be published elsewhere.

A similar situation exists in the glossophagine genus *Leptonycteris*, which on the North American mainland occurs from the extreme southwestern United States southward to Guatemala. Only one species was recognized in this region until 1962, when Davis & Carter pointed out that *L. sanborni*, named as a subspecies of *nivalis* in 1960, actually occurred sympatrically with the latter at a number of places in Mexico and could be distinguished from it by a combination of relatively minor characters including short, dense fur, nearly naked uropatagium, and smaller dimensions in certain external and cranial features. It is of note to point out here that differences of this magnitude frequently are thought to represent infraspecific variability (and, as a matter of fact, frequently do), when the bats in question are from different geographic areas. Only large series or, better yet, discovery of the two morphological types at the same geographic locality provide the clue that two different species actually are involved.

Recently, Phillips *et al.* (1969) have discovered additional characteristics that allow for easy recognition of museum specimens of the two North American species of *Leptonycteris*. *L. nivalis* has been found to possess a much less prominent presphenoid ridge than *sanborni*, and specimens of *nivalis* were found also to have unusual lesions or pits in the hard palate, adjacent to the upper premolars and frequently also the first upper molars. In extreme cases (about 14% of the bats studied), loss of teeth was associated with the lesions, which have been found in virtually all adults of *nivalis* examined from throughout the range of the species. In contrast, none of more than 430 specimens of *sanborni* examined had lesions or associated loss of teeth, even when they came from the same caves in which *nivalis* also was taken.

Pursuing this matter further, examination of the mouths of specimens of the two species preserved in alcohol revealed small clusters of a small macronyssid mite in the oral mucosa of *nivalis* at the places where lesions and pitting appear on the skulls (Fig. 8). Macronyssids were previously unknown internally in mammals or orally in any vertebrates.

Needless to say, the mite represents a new species, and its presence and the results of mite activity as seen on the cleaned skulls of *L. nivalis* represent an unusual kind of "taxonomic" character by which two sibling species of *Leptonycteris* can be readily distinguished. Of further interest is the fact that a similar situation lately has been found involving related species of two other glossophagine genera, *Anoura* and *Monophyllus*, where mites also seem to be host specific in one of a pair of related species.

Another sort of dental disease that could prove useful to systematists is the incidence of carious lesions in teeth. The only example presently available of this interesting feature (Phillips & Jones, 1970) involves two species of spear-nosed bats of the Neotropical genus *Phyllostomus* (*hastatus* and *discolor*) that are easily separable by a number of morphological characters. Examination of the teeth of these two species reveals an unusually high incidence (more than 40% of the individuals studied) of dental caries in *P. hastatus*, whereas no caries have been found in *P. discolor*. We have several ideas as to the reasons for a high incidence of caries in *hastatus*, but these are not germane to this particular discussion. What is of interest is that this sort of situation could be useful to systematists—(1) as a possible "taxonomic character" in the restricted sense, and (2) because it suggests some basic differences in fine tooth structure, or in environment of the mouth, or other ways in which the two species differ, and may prove useful in other groups where morphological differences between species are less distinct than in *Phyllostomus*.

A different set of problems exist where two closely related and morphologically similar species are not sympatric, and thus no direct evidence is available as to reproductive isolation or the lack of it. Such situations are best illustrated among insular populations, but are found also among mainland species. In these instances, morphological and other similarities and differences must be carefully assessed before a reasonable conclusion can be drawn as to whether or not the separate geographic segments represent the same or different species. One of the best examples that comes to mind involving a mainland group is the long-eared *Myotis* from the southwestern United States and northern Mexico that was described originally as only subspecifically distinct from *Myotis evotis*, another long-eared species that closely resembles it in both external and cranial features. Later, James S. Findley and his co-workers took specimens of both of these long-eared *Myotis* at Springtime Canyon, New Mexico, and they have since been found to be sympatric over a limited area in western New Mexico and eastern Arizona. Because the two long-eared siblings obviously represented

different species, and *evotis* was the older name, Findley (1960) opined that the populations in question evidently were members of the species of *M. keenii*, which they also resemble to a marked degree, but which occurs no closer to the geographic area than central Kansas. Having recently acquired a respectable series of these puzzling bats, we reviewed the entire question and concluded (Genoways & Jones, 1969) that the long-eared bats in question from the Southwest and Mexico actually represent a distinct species (*auriculus*), different in as many ways from *keenii* as from *evotis*, with which it is in geographic contact. Many of the differences are subtle, but in total are impressive. These include: differences in cranial morphology (Fig. 9) and in that of the molar teeth (Fig. 4); marked differences in the baculum (Fig. 7); and some rather slight differences in color and external proportions.

Considering island populations, the systematist cannot strictly apply the criterion of reproductive isolation or lack of it, because the related segments of a species or species-group already are more or less physically isolated on individual islands. In this situation, again, degree of morphological and other differentiation, in comparison with mainland variation among populations of the same or a related species, frequently is the only basis by which specific as opposed to subspecific status can be rationalized. A number of studies have appeared concerning variation in insular populations of bats, of which recent publications by Krzanowski (1967) and Phillips (1968) are of note. Schwartz & Jones (1967) studied the Antillean genus *Monophyllus* and reduced the number of recognized species from six to two. One, *M. plethodon*, is known from the Lesser Antilles and Puerto Rico, whereas the other, *M. redmani*, occurs throughout the Greater Antilles. The two species are closely related, differing only in the position of the first two upper premolars. However, both species evidently occurred together on Puerto Rico as late as sub-Recent times (see also Choate & Birney, 1968), and character displacement may have taken place there. The same authors (Jones & Schwartz, 1967) reviewed the status of the Lesser Antillean genus *Ardops*, reducing the four known monotypic species to subspecific status under *A. nicholli* "because (1) the differences between them are slight and quantitative in nature, (2) overall variation does not exceed that described as occurring in a number of other polytypic species of sternodermine genera, and (3) such a classification best reflects the similarities and obviously close affinities of the included taxa." They went on to point out that: "A continuum in size can be demonstrated among the five subspecies but the continuum is not clinal, suggesting that the various insular populations have adapted independently to conditions prevailing on individual islands."

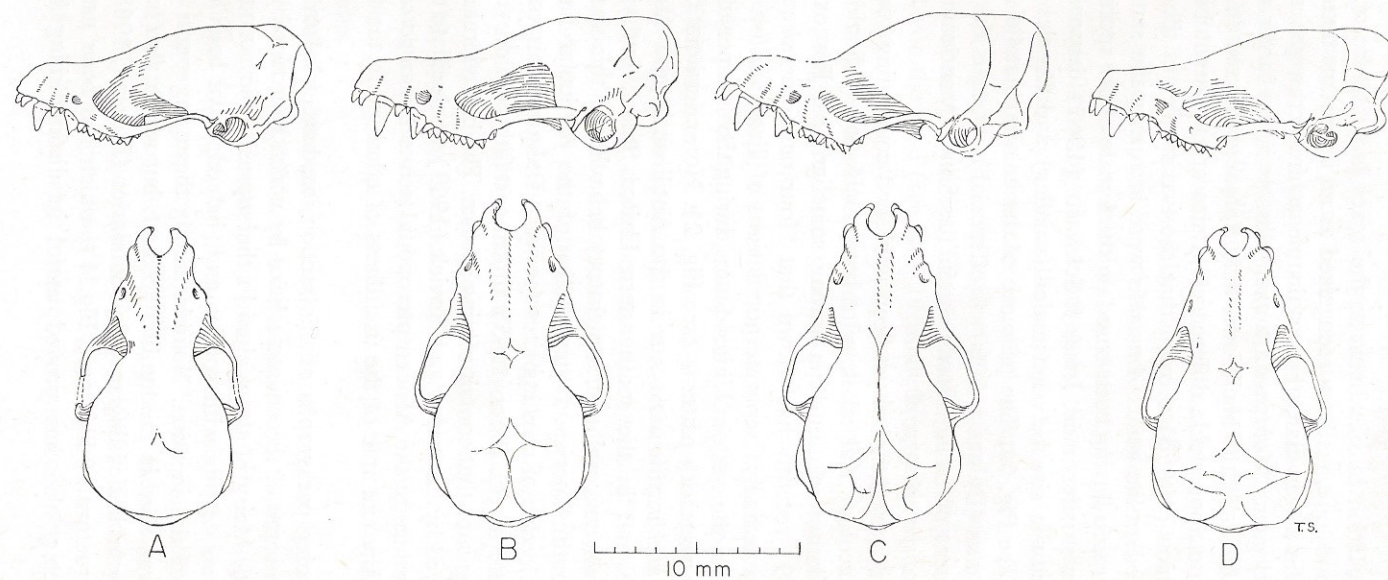


FIG. 9. Lateral and dorsal views of crania of four related species of *Myotis* showing differences in size and proportions: A, *Myotis milleri*; B, *Myotis evotis*; C, *Myotis auriculus*; D, *Myotis keenii*. (After Genoways & Jones, 1969).

Secondary variation in size between the sexes is a feature of some groups of bats and long has been recognized as an important taxonomic consideration; the larger males in certain megachiropteran genera and in the free-tailed genus *Molossus* are examples, as is the larger size of females in the New World big brown bat, *Eptesicus fuscus*. In many bats, however, no appreciable differences in size are apparent between the sexes. Peterson (1965b) showed that the two species of the South American sternodermine genus *Ametrida* were in reality the same bat, the name *A. centurio* having been based on the female of the species and *A. minor* on the smaller male. Jones & Schwartz (1967) demonstrated a similar disparity in size between males (smaller) and females in the genus *Ardops* (see Fig. 6). The presence of the unique "natalid organ" in males of *Natalus* (Dalquest, 1950) is of special note, as is the differential development of facial adornment in the South American steno-dermine *Sphaeronycteris toxophyllum*.

Although relatively little has yet been published concerning comparative aspects of ecology and ethology of bats, such studies should prove useful in elucidating relationships among some groups. For example, Cockrum (1969) recently has shown that "four or more behaviorally (and possibly genetically) separate populations of *Tadarida brasiliensis mexicana* occur in the western United States during the summer months" on the basis of migratory patterns (see Fig. 2). Non-migratory populations of *Tadarida brasiliensis* occur in the Antillean region (Jones & Phillips, 1970) and in the southeastern United States, but virtually nothing is known concerning the migratory behavior of this species in Middle and South America. Other studies of the particular habits of bats, such as selection of roosting sites (see also Dalquest, this volume), and activity patterns (C. Jones, 1965) almost certainly will prove useful in considering groups that contain sibling species. The behavioral characteristics employed by Lawrence and Novick (1963) to elucidate the systematic relationships of the African pteropodid genus *Lyssonycteris* provide a noteworthy example of the usefulness of ethology to the taxonomist.

In the foregoing paragraphs of this section, we have tried to allude, by example, to some of the characteristics by which reproductive isolation is detected. Many of those cited in the supraspecific accounts are useful also when dealing with species and, indeed, have been used at several levels of classification. Notable among these are sperm morphology, which was cited in the familial account, but which also has been shown to be useful in defining specific boundaries (Forman, 1968). The microscopic structure of hair (see Fig. 1), which has been used as a generic character, also has proved useful in distinguishing between

species (Benedict, 1957; Dwyer, 1962; Miles, 1965; Nason, 1948). The baculum or os penis bone, mentioned briefly above, is of considerable interest. This structure is present, albeit usually small, in most groups of bats, although the bone is absent in all members of the families Noctilionidae and Phyllostomatidae thus far examined. An interesting situation exists in the molossid genus *Eumops*, members of which generally are characterized by the presence of a baculum; of the two largest representatives, *E. perotis* and *E. underwoodi*, the former lacks a baculum whereas the latter has a relatively large bone (Brown, 1967). The female homolog of the baculum, the os clitoridis, has not been studied as extensively as has the os penis, but also may be found to be a valuable taxonomic character in some groups.

Certain aspects of the soft external anatomy of bats have been widely used in taxonomic studies. The structure and arrangement of fleshy outgrowths on the nose (see Hill, 1963, on *Hipposideros*, for example) and face of some bats are of import, as is the structure of the tragus (see Peterson, 1968, on *Vampyressa*, for example), ears, wing membranes, and uropatagium, and the distribution and development of glandular masses, among others.

We do not intend to discuss infraspecific variation at length, but it should be pointed out that subspecies of a given species characteristically differ in many of the same ways as do different species, if not to the same degree. Subspecies, however, are distinguished from species in that under natural conditions the subspecies of a given species are actually or potentially capable of interbreeding. Such features as color, size, minor cranial proportions, even presence or absence of teeth, as in certain species of the phyllostomatid genus *Artibeus* (Handley, 1965; Jones & Phillips, 1970), and in the *Myotis lucifugus* complex (Findley & Jones, 1967), may vary geographically within a single species (see Table 1). In many instances such variation is clinal, that is to say, various characters, coat color or size for example, change gradually from place to place as a result of adaptation to local environmental conditions.

Studies of infraspecific variation are of interest because they reveal the extent of adaptation of local populations to the environment, and sometimes reveal trends in variation in the chronologic history of a species. One frequent by-product of such studies is the discovery that two or more geographically segregated "species" really represent only well-marked races of one widespread species (see, for example, Hall & Jones, 1961, and Anderson & Nelson, 1965). Studies of infraspecific variation, as all other studies of bat systematics, have been greatly aided in recent years by the large series of specimens of many species, formerly

TABLE 1

Selected measurements (in millimeters) and presence or absence of the third upper molar (M3) in samples of *Artibeus jamaicensis* from several of the southern islands in the Lesser Antilles and from Trinidad. Islands are arranged from north to south in order to clearly illustrate infraspecific variation in size and in the condition of the M3. Sample size is indicated to the left of each mean measurement; extremes are in parentheses. For M3, sample size and percentage of specimens having the tooth are given. (After Jones & Phillips, 1969).

Island	Forearm	Condylbasal length	Zygomatic breadth	Per cent M3 present
<i>Artibeus jamaicensis jamaicensis</i>				
Barbados	7 58.9(55.6-62.1)	7 25.3(24.9-26.1)	7 17.6(17.2-17.9)	7 0
St. Lucia	11 60.1(56.5-64.0)	15 26.1(25.4-26.7)	15 17.7(17.1-18.1)	17 0
<i>Artibeus jamaicensis</i> , new subspecies				
St. Vincent	20 64.3(60.5-67.4)	32 27.3(26.2-28.6)	32 19.4(17.9-20.6)	35 12*
<i>Artibeus jamaicensis trinitatis</i>				
Grenada	23 58.1(55.8-60.5)	15 25.0(24.7-25.8)	15 17.5(17.1-18.2)	18 94
Trinidad	16 57.3(55.1-61.7)	11 24.2(23.4-25.0)	11 17.4(16.8-18.5)	12 100

*Two of four specimens had but one M3, on the right side in each case.

considered rare, that have accumulated as a result of the use of mist nets and other types of traps for bats. For additional representative studies of infraspecific variation see W. H. Davis (1959), Handley (1959), Paradiso (1967), and W. B. Davis (1968, 1969), among others.

It should be mentioned, too, that application of computer techniques and multivariate statistics, little used as yet in studies of Chiroptera, will greatly enhance consideration of geographic variation as well as assessment of relationship at higher levels of bat classification. Numerical analyses surely will occupy a prominent place in the study of chiropteran systematics in years to come.

SUMMARY

In the foregoing pages we have attempted, in the spirit of this symposium, to provide an overview of the field of chiropteran systematics in a way that will introduce the non-chiropterologist to the subject. By way of example, we have alluded to several aspects of taxonomic research at different levels in the hierarchy. Recourse to the publications cited at the appropriate places in the text will amplify our remarks and provide a solid background in the current work of the discipline.

Basically, taxonomic characters are where the taxonomist finds them; some, but not all, will prove useful also in elucidating relationships and evolutionary descent of taxa. Much remains to be done in these areas, as our discussion hopefully indicates. We would again remind the reader that each of the other papers in this volume can be related, in one way or another, to the overall problem of classification and systematics of bats.

Museum of Natural History, The University of Kansas, Lawrence, Kansas 66044.